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HOME RANGE DYNAMICS OF MOUNTAIN HARES (*LEPUS TIMIDUS*) IN THE SWISS ALPS

ANNE-SOPHIE GENINI GAMBONI¹, FRANCESCO BISI²,
ELISA MASSERONI^{2,3}, MOSÈ NODARI², DAMIANO G. PREATONI²,
LUCAS A. WAUTERS², ADRIANO MARTINOLI², GUIDO TOSI²

¹6714, Semione, Switzerland

²Department Environment-Health-Safety, University of Insubria Varese, Via J.H. Dunant 3,
21100 Varese, Italy

³Institute Oikos NGO Via Crescenzago 1, 20134 Milano, Italy

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ABSTRACT - Little is known on the ecology and behaviour of the alpine mountain hare (*Lepus timidus*). Between 1996 and 1997, we analysed by radiotracking the pattern of space use of 8 mountain hares from the Swiss Alps. We estimated home range size using both the kernel density estimator and the minimum convex polygon. We found smaller ranges (38 ha) compared to those reported for the species in boreal or arctic habitats, but similar to ranges in Scotland. Hares did not use a centre of major activity (core area) and showed high home range overlap, confirming their non-territorial behaviour. Smaller ranges were used during winter compared to the other seasons, whilst no difference in size was found between sexes.

Key words: *Lepus timidus*, mountain hare, home range, core area, alpine ecosystem

RIASSUNTO - *Dinamica dell'uso dello spazio della Lepre bianca (Lepus timidus) nelle Alpi Svizzere.* Le informazioni relative all'ecologia e al comportamento della lepre alpina (*Lepus timidus*) sono ad oggi scarse. In questo studio abbiamo analizzato l'utilizzo dello spazio di una popolazione di lepre bianca sulle Alpi Svizzere. Tra il 1996 e il 1997 sono stati marcati con radio collare 8 individui di lepre alpina. L'*home range* è stato calcolato utilizzando lo stimatore di densità kernel (KDE) e il metodo del minimo poligono convesso (MCP). L'ampiezza degli *home range* (38 ha) è risultata inferiore a quella riportata per la specie in habitat boreali e artici, ma simile a quella riscontrata in Scozia. All'interno dell'*home range* non è stato rilevato alcun centro di maggiore attività (*core area*) ed è stata evidenziata una notevole sovrapposizione tra gli stessi, confermando la non territorialità della specie. Le aree frequentate in inverno sono risultate più piccole rispetto alle altre stagioni e non sono state riscontrate differenze tra i sessi.

Parole chiave: *Lepus timidus*, Lepre alpina, home range, *core area*, ecosistema alpino

INTRODUCTION

The mountain hare (*Lepus timidus* Linnaeus, 1758) is a Palearctic relict species with a wide distribution area,

from Ireland and Scandinavia in the west, across Siberia, Mongolia and China to the northern islands of Japan in the east (Angerbjörn and Flux, 1995). In Europe, isolated alpine

populations of *Lepus timidus* occur above 1300 m a.s.l. in the mountains of France (Couturier, 1964), Germany, Switzerland, Austria, Slovenia (Isakovic, 1970) and Italy (Mitchell-Jones *et al.*, 1999). Although the ranging and spacing behaviours of the mountain hare have been studied in Scotland (Hewson, 1976; Hewson and Hinge, 1990; Hulbert *et al.*, 1996) and Scandinavia (Hiltunen *et al.*, 2004; Dahl, 2005a, b; Kauhala *et al.*, 2005; Hiltunen, 2006), little is known about the social structure and home range characteristics of alpine mountain hare *Lepus timidus varronis*. In contrast with the large, contiguous boreal or arctic habitats occupied by mountain hares in the northern part of their range, the distribution of suitable habitats in the Alps (sub-alpine coniferous forest, alpine shrub and meadows) is heterogeneous and patchy (our unpubl. data). This difference in landscape structure is likely to affect home-range size and overlap.

Here we analyse the pattern of space-use of eight mountain hares that were radio-tracked in the Swiss Alps in 1996, comparing data on home-range size and overlap with the spacing patterns described for populations from Scotland and Scandinavia.

STUDY AREA AND METHODS

Mountain hares were studied in the Blenio Valley (46°28' N, 8°53' E) - Ticino Canton, southern Switzerland -, between 1500 and 2050 m a.s.l. The habitat is characterised by typical alpine vegetation with alpine grasslands (59%), clearings and landslide cones (19%) and Norway spruce forest (22%).

Between November 1995 and October 1996, eight mountain hares were trapped using hand-made traps of three different kinds: wooden traps (62 x 58 x 125 cm) and aluminium traps (60 x 60 x 125 cm and 60 x 40 x 120 cm). Hares were radio-collared with adjustable necklace transmitters (L-I/ER3, article S212, A. Wagener, Köln, Germany) weighing 35g. Radio-tagged hares were located using a Yaesu receiver (148-149 MHz, FT-290R II., Yaesu Musen Co., Ltd., Tokyo, Japan) and a three-elements directional Yagi antenna. The animals were localised by triangulation (White and Garrott, 1990) once a week, taking one fix every 15 minutes for two hours, in order to cover periodically the whole 24 hours. At each fix, hares' location and activity (1 = active, 2 = not active) were recorded.

We did not test for independence of subsequent fixes, since, using a fixed study period, concerns regarding autocorrelation are relatively unimportant compared to obtaining a representative sample of fixes to reliably estimate home range size (Otis and White, 1999; Fieberg, 2007). For example, to subsample observations that are equally spaced throughout the study period would only decrease the precision of home range and the estimates of the utilisation distribution (UD) (Fieberg, 2007).

We estimated home ranges at a seasonal level: winter (December-March, ground continuously covered with snow), spring-summer (April-August, corresponding to hare "breeding season" and vegetation growth), and autumn (September-November, post-breeding season). We used the R software (R Development Core Team, 2007) for all analyses. We calculated the fixed kernel density estimator (KDE; Worton, 1989; Seaman and Powell, 1996) with adjusted smoothing factor (KDE with hadj), following the method proposed by Wauters *et al.* (2007) to calculate hadj. For comparison with

previous studies, we also calculated home range size with the minimum convex polygon (MCP) using the recalculated arithmetic mean and compared the two methods – KDE and MCP –, by the Wilcoxon matched-pairs signed-ranks test. Internal home range structure was explored for a core area of high activity (Kenward, 2001), examining the UD (range size included in 5% incremental isopleths containing between 20% and 95% of fixes) of the fixed kernel density estimator (KDE; Kenward, 2001). A one-way ANOVA was applied to define the core area, with the size of hares' range included in a given isopleth as dependent variable and the 5% incremental isopleths as class.

Home range overlap was expressed as the percentage of a hare's range overlapped by those of all other hares (e.g. Wauters and Dhondt, 1992; Lurz *et al.*, 2000). Values are presented as mean \pm standard deviation (S.D.).

We investigated the effect of season (1 = winter, 2 = spring-summer, 3 = autumn) and sex on home range size using the 95% KDE estimator (Kenward *et al.*, 2001; Wauters *et al.*, 2005, 2007; Di Pierro *et al.*, 2008) with a two-way ANOVA (Proc mixed; SAS, 1999). When necessary, home range data were ln-transformed to meet the assumptions of normality (Shapiro-Wilk's test $W > 0.93$, $P > 0.3$). To account for pseudo-replication of repeated measures, "individual" was added as a repeated factor. Models with simple correlation structure of the residual correlation matrix, corresponding to no effect of repeated measures on the individual, had the smallest values of Schwarz's Bayesian Information Criterion (BIC), indicating the best fit (Verbeke and Molenberghs, 2000).

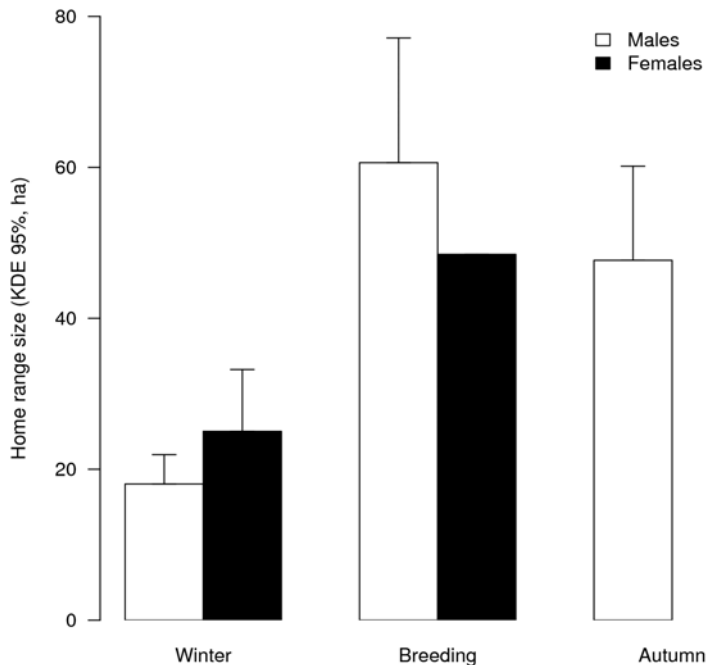
RESULTS AND DISCUSSION

We used 13 seasonal home-range estimates from eight different hares, six males (3 sub-adults, 3 adults) and two

adult females. For each individual, 95% KDE estimates of home-range size were larger than 95% MCP (Wilcoxon matched-pairs signed-ranks test: $P = 0.0005$, 95% KDE mean = 38.1 ± 23.7 ha, min-max = 11.9-77.2 ha; 95% MCP mean = 26.7 ± 21.6 ha, min-max = 2.5-64.1 ha, Tab. 1). Home range size (95% KDE) did not differ between the two sexes (Sex-effect: $F_{1,9} = 0.27$, $P = 0.61$), but was smaller in winter than in the other seasons (Season-effect: $F_{2,9} = 7.02$, $P = 0.015$, Fig. 1, 2). Due to the small sample size, we cannot draw any general conclusion about sex-specific space use patterns in alpine habitats. The use of small home ranges in winter might be a strategy to reduce energy expenditure during a season with critical weather condition, such as low temperatures (mean monthly $T < 0^{\circ}\text{C}$) and deep snow cover. In comparison with other studies, home range sizes in the Swiss Alps were smaller than in Scandinavia (min-max = 71-280 ha; Hiltunen *et al.*, 2004; Dahl, 2005a, b; Dahl and Willebrand, 2005; Kauhala *et al.*, 2005; Hiltunen, 2006), but similar to those documented in Scotland (min-max = 15-113 ha; Hewson and Hinge, 1990; Hulbert *et al.*, 1996, Rao *et al.*, 2003). In Scotland (moorlands) and alpine environments (mountain pine or other forests) a homogeneous distribution of food resources in sufficiently large patches might explain the reduced movements when searching for food or hiding places, and, consequently, the use of relatively small home ranges. We found only one other study, in Austria, on the ecology of alpine populations of this species (Slotta-Bachmayr, 1998), that reported average home ranges of 435 ha (95%

Table 1 - Seasonal home range size in hectares calculated for each hare by the kernel density estimator (KDE) and the minimum convex polygon (MCP).

| Hare code | Season | No. locations | 95% KDE | 95% MCP |
|-----------|----------|---------------|---------|---------|
| 9001 | Autumn | 99 | 26.9 | 7.7 |
| 9001 | Winter | 245 | 15.9 | 11.6 |
| 9002 | Winter | 693 | 16.8 | 12.4 |
| 9003 | Winter | 950 | 29.4 | 20.4 |
| 9003 | Breeding | 58 | 27.6 | 2.5 |
| 9004 | Winter | 264 | 11.9 | 8.4 |
| 9005 | Winter | 1045 | 33.2 | 19.7 |
| 9005 | Breeding | 1353 | 48.5 | 49.5 |
| 9006 | Breeding | 2178 | 77.0 | 60.6 |
| 9006 | Autumn | 954 | 46.1 | 40.1 |
| 9007 | Winter | 566 | 15.1 | 8.3 |
| 9009 | Breeding | 1881 | 77.2 | 64.1 |
| 9009 | Autumn | 557 | 70.0 | 41.3 |

Figure 1 - Seasonal home range size in hectares (mean \pm S.E.): winter (4 males, 2 females), breeding season (3 males, 1 female), autumn (3 males).

MCP) and 551 ha (95% KDE), hence, much larger than in our study. However, the period over which each hare were monitored was not clearly defined (entire study period from November 1992 to March 1996), and hares made exploratory movements over wide areas (Slotta-Bachmayr, 1998) that could introduce bias in home range estimation.

Exploring the use of a core area, no significant increase in range area was observed in any pair wise comparisons between consecutive contours (Tukey's test on differences between means, all $P > 0.05$). Hence, no area of concentrated use could be detected. Accordingly, day-time radiotracking showed that each animal used several forms, widely spaced throughout its home range (our unpubl. data).

The average percentage of home range

overlap between mountain hares was $51 \pm 22\%$ ($N = 44$, min-max: 14-100%). Mean overlap between male ranges was $52 \pm 24\%$ ($N = 17$), of a male by females was $49 \pm 17\%$ ($N = 7$) and of a female by males was $47 \pm 22\%$ ($N = 8$). The large home range overlap found in this study supports the hypothesis that the mountain hare is a non-territorial species, as documented in several study areas of northern Europe (Flux, 1970; Hewson, 1976; Hewson and Hinge, 1990; Dahl, 2005b).

Ecosystems are rapidly changing due to human activities and global warming (Stenseth *et al.*, 2002; Walther *et al.*, 2005; Thomas *et al.*, 2006). Studies on a wider range of populations, living in different habitat types, of the alpine mountain hare are necessary to better understand the social organisation and habitat use of this keystone species for alpine ecosystems.

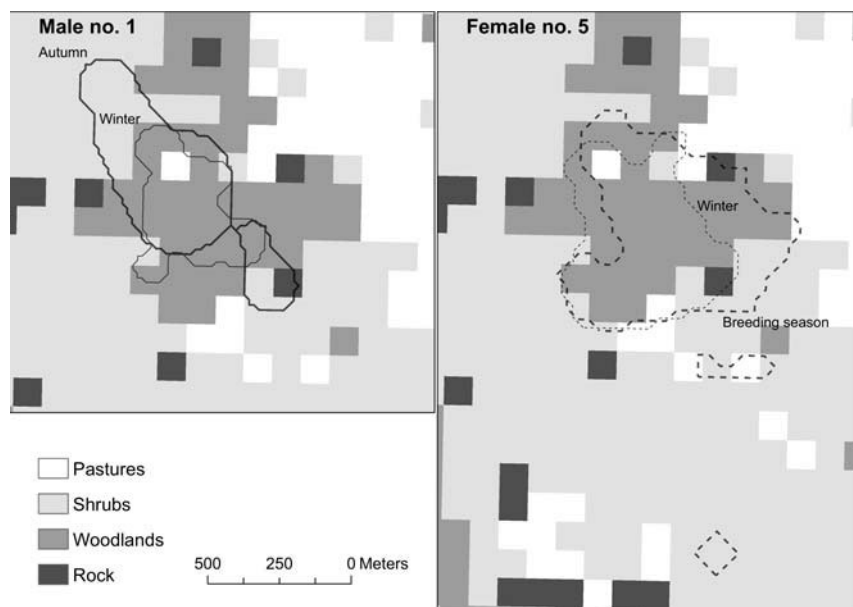


Figure 2 - Home ranges of two mountain hares (male no. 1: continuous lines and female no. 5: dashed lines) in different seasons. Thin lines: winter home range; thick lines: autumn and breeding season for male and female respectively.

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